Three brown frog species in Denmark have different abilities to colonise new ponds

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Abstract

For 29 consecutive years, the populations of three species of brown frogs, *Rana arvalis*, *R. dalmatina* and *R. temporaria*, were monitored in an open area in South Zealand, Denmark, with no direct influence of agriculture. Population sizes were recorded by counting egg clumps and showed large variations from year to year. The total population of *R. arvalis* differed by a factor of 100 between the years with the lowest and the highest numbers. A total of 19 initially unoccupied suitable waterbodies could potentially be colonised by the frogs. *Rana dalmatina* colonised all of the ponds, mostly in the very first year of existence. *Rana arvalis* colonised 17 ponds after an average of 10.5 years. *Rana temporaria* colonised eight ponds after an average of 13.4 years. Colonisation by *R. dalmatina* was independent of changes in total population size, whereas colonisation by *R. arvalis* predominantly occurred in years with considerable population increases. The results are discussed in relation to the movement patterns and philopatry of juvenile frogs of the three species. Juvenile *R. dalmatina* disperse far from the breeding site, but most individuals return to their natal site. This allows the species to be an efficient coloniser of new waterbodies and, at the same time, to have stable occurrence at the original site. The two other species show a more erratic type of dispersal and especially *R. temporaria* often shifts breeding site from year to year.

Key Words

dispersal, movements, philopatry, *Rana arvalis*, *Rana dalmatina*, *Rana temporaria*, time series

Introduction

This paper reports the results from monitoring of brown-frog populations covering a 29-year study period. The purpose is: 1) to present a long data series on the development of amphibian populations in an area where populations were not threatened by the influence of agriculture and 2) to report differences between species in colonisation events.

The study was conducted in a military training area in South Zealand, Denmark. Three species of brown frogs breed in this area: moor frog, *Rana arvalis* Nilsson, 1842, agile frog, *Rana dalmatina* Fitzinger in Bonaparte, 1838 and common frog, *Rana temporaria* Linnaeus, 1758.

Brown frog population size was monitored by counting the number of egg clumps in spring. Each mature female will usually produce a single egg clump per year in *R. dalmatina* (Hachtel and Grossenbacher 2014) and presumably also in other *Rana* species (Glandt 2014). Thus, the total egg clump count approximately indicates the number of mature females and, thereby, provides a population size index.

Several other studies have reported long-term monitoring results for European species of brown frogs by egg clump counts (Meyer et al. 1998; Hartel 2008; Ahlén 2013; Băncilă et al. 2016; Canova and Balestrieri 2018; Combes et al. 2018; Meek 2018; Schmidt et al. 2021). However, in all these studies, the study species was distributed in a way that left little opportunity to study colonisation events.

In the present study, populations were monitored in all waterbodies in an area covering nearly 2 km². During the

study, 19 new suitable waterbodies were created or arose by natural flooding, which allowed monitoring of how fast each of the three species colonised waterbodies that had become available for breeding.

It is well known that amphibians are declining (e.g. Fog (1988)) and that the most efficient way to counteract such decline is the creation and improvement of ponds (Fog 1997a). Many projects in European countries have been conducted to improve the living conditions for threatened amphibian species by restoring old ponds and/or creating new ones. The largest efforts have probably been made in Switzerland, The Netherlands and Denmark (Fog 1997a; Stumpel and van der Voet 1998; Fog et al. 2019; Moor et al. 2022). In Denmark, for instance, thousands of ponds have been created since 1988. A survey of follow-up data (Fog 1997a) provided the results for 1,308 ponds. These were investigated again 5 years after the improvement. By then, 43% of the new ponds and 42% of the restored ponds had been colonised by natural immigration of the target species.

The colonisation process depends on several aspects of the species' biology, such as pond fidelity and the number of individuals that move far away from their natal pond. The importance of such traits is extensively discussed in literature on amphibian ecology, for example, by Smith and Green (2005) and Sinsch (2014). The present paper may add new aspects to that discussion.

Methods

Study area

I conducted the study in the military training area of Kulsbjerge in South Zealand, Denmark, situated at 55°N, 12°E (Fig. 1). The training grounds, comprising a total area of 4.96 km², were established in 1970. Before this, the area was used for intensive agriculture.

The study area covers about 1.8 km² in the eastern half of the military training area. It is hilly with elevations ranging from 50 to 100 m above sea level. The terrestrial habitats are mostly grassy vegetation with a height of less than 1 m. Many bushes are scattered around, mainly *Crataegus* and *Salix*. To the north, the study area is bordered by deciduous wood; to the south, mostly by detached houses with gardens. To the east and west, the military area extends beyond the study area.

Until 1970, only few possible breeding localities existed for amphibians in this area: a few small marl pits and a few larger swamps formed by peat diggings. The many depressions in the landscape were kept dry by drainage pipes. In the period up to 1992, when the study started, additional waterbodies had arisen, mostly as flooding in natural depressions after heavy military vehicles had destroyed the drainage pipes in the ground. The largest natural flooding covered 8,000 m². Water depth and vegetation vary amongst the waterbodies. Many of them have extensive reed belts of *Typha latifolia* along the banks. A few of the waterbodies have fish, but the fish species were

not determined, except that pikes (*Esox lucius*) were observed in two waterbodies and a dead tench (*Tinca tinca*) was seen in another. Over the years, predation pressure from fish has varied. After some winters with long ice cover and after desiccation in dry summers, fish populations were reduced, after which breeding frogs immigrated into the respective waterbodies.

Out of the waterbodies that existed in the area in 1988, two were lakes with fish. Eleven were permanent waterbodies with no fish or moderate fish populations. These waterbodies were not changed further and were not defined as targets of colonisation. At the start of the study, 10 of them were inhabited by *R. dalmatina* already, seven by *R. arvalis* and five by *R. temporaria*. The latter species colonised some waterbodies that had existed unchanged all the time, but were not inhabited until some time had passed after the study period had started. Such cases were not included in data on colonisation, because it was not possible to indicate the number of years since the first existence of those waterbodies.

In 1988, the military administration agreed that a number of ponds were excavated or improved to benefit amphibians. Improvements comprised cutting down shading trees, removing bottom sludge by dredging and improving bottom profiles to create more gently-sloping banks. In these ways, a total of eight new or improved ponds were made in the years 1989 and 1992. Three of these were colonised by *R. dalmatina* already before the improvement. Thus, the remaining five ponds could potentially be colonised in the following years by this species and all eight ponds could potentially be colonised by the two other brown frog species. There were no fish in these ponds, except that a pike was observed in one of them, but this did not prevent subsequent colonisation there in the shallow parts by *R. arvalis* and *R. temporaria*.

During the 1992–2020 study period, many more floodings formed in natural depressions. Here, the term "flooding" indicates a depression that was previously dry, but which gradually became inundated with rainwater. These floodings were not in contact with streams or lakes and did not have fish. Eleven of them gradually turned into permanent waterbodies. For three of these 11, the first year when they could possibly be colonised was ambiguous, for instance, when they came into existence in one year, then were dry for several years and later came into existence again. For the remaining eight waterbodies, the first year of existence was well defined. One flooding was already colonised by *R. dalmatina* when the study started.

To sum up: altogether, 19 waterbodies where *R. arvalis* and *R. temporaria* were initially not present, could potentially be colonised by them. All of these 19 waterbodies are considered to be suitable for breeding of all three brown frog species. In four of these ponds, *R. dalmatina* was already present before the start of the study period, so only 15 vacant waterbodies were available for colonisation by *R. dalmatina* during the study period.

Fourteen other floodings formed during the study period, but these existed only in some years and were,

Figure 1. The location of the study area in south Zealand is marked with a red dot.

therefore, not considered suitable for permanent colonisation. Altogether, the number of waterbodies that existed in all years, or in most years, or in only some years, were 2 + 11 + 19 + 14 = 46. Eggs were also found in very temporary floodings that dried out a few weeks later and did not turn into permanent ponds in subsequent years. I did not classify such cases as colonisations, because no new breeding population could be established there. Such places were not included in the counts of waterbodies.

Detecting colonisation

I inspected all excavated and improved ponds annually to register when eggs of a species appeared for the first time. I inspected natural floodings even if they had just arisen and there was only little water. The first time that an egg clump of a species appeared was noted as "first appearance". If this was followed by continued presence of the species in some of the following years, this was classified as "colonisation". The first parent generation might have died after the first year, but if new egg clumps were found no later than 4 years after, this could possibly represent the breeding of the offspring from the previous eggs and so this was also classified as a colonisation. If the species had colonised the site continuously during a few years and then disappeared again, this was also considered as a colonisation.

Recordings

After a few observations in 1988 and 1990, I initiated systematic recordings in 1992. Each year, I surveyed all relevant waterbodies in the study area for *Rana* eggs, except that a few ponds were omitted in 1992 and a few others in 1993. The number of survey dates per year was 3–5, depending on the total number of egg clumps and, hence, how many days were necessary to investigate

all waterbodies. Each locality was investigated first for *R. dalmatina* and then once again for the two other species, which breed slightly later in the spring. Six to 22 days passed between the first and the last visit. The number of visits depended on how concentrated the spawning season was in that particular year.

Very often, repeated visits of the same waterbodies were made to check if the first counts gave the full number of egg clumps or if additional egg clumps had been spawned later in the season. Data from such repeated visits allowed me to compare the results from a first and a second visit in the same spring of the same waterbody and also gave interesting information on the length of the spawning period in different years.

The search for *R. dalmatina* egg clumps was conducted by wading through all accessible parts of the waterbodies to a water depth of approx. 1.2 m and recording all egg clumps that could be seen from there. In most waterbodies, the search route followed a meandering pattern with a distance of 2–3 m between parallel tracks. During the recordings, some egg clumps remain fixed to straws at a depth of up to 1 m below the water surface. To detect such clumps, full sunshine is crucial, as half or more of the clumps below the water surface will be overlooked in overcast weather.

Egg clumps of *R. arvalis* and *R. temporaria* were usually, but not always, deposited in shallow water near the banks. They are typically placed so densely together in shallow water near banks the that they form "egg carpets". Some clumps were detected at the bottom at depths of more than 50 cm or in floating vegetation far from the bank while searching for *R. dalmatina* clumps. Counting clumps in egg carpets required full sunshine to clearly identify borders between different clumps. If the eggs formed dense carpets, I lifted upper egg clumps to observe any additional clumps below them. In a few cases, when egg carpets were large and extensive, I measured the area of the egg carpet with a folding ruler and calculated the number of clumps from previous observations of number of clumps per m². For *R. arvalis*, this was most often ca. 100 clumps per m².

The results may be considered as an index of the population size. As I made all observations in the same waterbodies in the same manner and in the same weather conditions (full sunshine) every year, differences between years are a reliable indication of differences in this "index value".

The main focus of the present study is colonisation. Here, the crucial data are presence or absence of the species rather than the exact population size. Newly arisen waterbodies had clear water, sparse vegetation and were often shallow. In such waterbodies, it can be assumed that 100% of the egg clumps had been detected.

Species determination

Species determination from egg clumps is not straightforward and requires experience. Description of specific characteristics of egg clumps, for example, in Nöllert and Nöllert (1992), do not generally hold true for all sizes of spawning females or in all geographic regions. Egg clumps of *R. dalmatina* are usually very characteristic, being fastened around submerged vertical straws. However, in case they are not, they may be determined from the structure of the egg gel and by the characteristic shape of the embryos shortly before hatching. At the beginning of the project, I placed a few eggs from egg clumps at Kulsbjerge in aquaria and reared them until the tadpoles were large enough to tell the species, in order to define what characterises egg clumps of the species in this local area. I concluded that distinguishing the egg clumps of *R. temporaria* from those of *R. arvalis* was usually possible, though not always. No single character will ensure a 100% certain determination. The most useful character is that the egg gel is firmer in *R. arvalis* than in *R. temporaria*. Furthermore, the colour hue is often, but not always, a useful characteristic.

In the Kulsbjerge area, *R. arvalis* and *R. temporaria* usually deposit their eggs mixed between each other in the same egg carpets. It is difficult to determine which clumps belong to each of the two species. Determining this requires the handling of every single egg clump to feel the firmness of the gel. In cases of doubt, I used additional options, for example, inspection of the egg clumps just when the newly-hatched larvae lie on top of the egg mass. In this stage, *R. temporaria* and *R. arvalis* differ by the length of the external gills (Fog et al. 2001; Pankratius and Assmann 2008). A further possibility is to catch tadpoles in the water later in the season and determine their species from the teeth rows in the mouth field, as described, for example, in Grillitsch et al. (1983), Nöllert and Nöllert (1992) and Fog et al. (2001). In some cases, I observed newly-metamorphosed froglets at the water's edge. Fog (2008) has described which characteristics are useful in identifying *R. dalmatina*, *R. temporaria* and *R. arvalis* froglets. The species of froglets found always matched the species of eggs found in the spring.

Catching of adult frogs or hearing them calling was possible in only a few cases.

Determinations of *R. dalmatina* are here treated as being always correct. Most, but not all, determinations of *R. arvalis* and *R. temporaria* are considered to be certain. I noted some egg clumps as "likely *R. temporaria*". Data on such egg clumps were used only in the presentation of the overall population trends, not for recordings of colonisation. Furthermore, a few egg clumps remained "undetermined"; this included some egg clumps that had dried out before I found them.

Differences in how rapidly species colonise

For each waterbody and for each of the three species, I recorded the length of the period (the number of years) until the species appeared there for the first time and until it had more permanently colonised the waterbody. A Kruskal-Wallis test was used to test for differences between

the three species in the duration until appearance or until colonisation and, subsequently, a Wilcoxon-Mann-Whitney test was used as a post-hoc test for pairwise comparisons between two species. The calculations were made manually following the procedures given by Siegel and Castellan (1988).

It was of interest to examine if colonisations occurred mainly in years with large population increases. I chose an arbitrary criterion for what was a year with a large increase, namely that the increase in population size from the previous year was at least 50% of the average population size over the study period for that species. This reflects the absolute number of new recruits in the area, which is more relevant than the relative number of new individuals compared to the previous years. This criterion selected a suitable number of years, namely 5, 6 and 5 years, respectively, for *R. dalmatina*, *R. arvalis* and *R. temporaria*. Next, the probability that a particular colonisation event randomly occurred in one of these years, was calculated as follows: for each species and each year, the number of previously unoccupied waterbodies that could potentially be colonised was counted and the total number of colonisation opportunities that fell within the indicated 5 or 6 years was calculated as a proportion of all opportunities. For instance, in *R. arvalis*, a fraction of 0.198 of all colonisation opportunities fell within the 6 years referred to. Taking this as the probability in a binomial distribution, I used the binomial test for the H_0 hypothesis that the sum of the number of colonisation

events in these selected years was no higher than expected, using the total number of colonisation events as the number of trials in the distribution.

Results

Population sizes

During the 29-year observation period, in all waterbodies combined, a total of approx. 60,000 egg clumps were counted, amongst which 35.6% were *R. dalmatina*, 55.5% were *R. arvalis* and 5.9% were certain *R. temporaria*, 1.2% were likely *R. temporaria* and 1.7% were undetermined (Suppl. Materials 1, 2). Populations were relatively small during the 1992–2003 period and considerably larger during the 2004–2020 period (Fig. 2). For *R. dalmatina*, the minimum number of egg clumps was 279, recorded in 2003. The maximum number counted was 2,179, recorded in 2020. The minimum number of reliably determined *R. arvalis* was 23, recorded in 1994, to which must be added most of the 39 undetermined egg clumps. The maximum number of *R. arvalis* egg clumps was 4,310, recorded in 2013. *Rana temporaria* had a maximum of 691 in 2020. There were no certain recordings of *R. temporaria* from 1995 to 2002, but, in most of these years, there were likely recordings or (in 1996) undetermined eggs that could also have been *R. temporaria*. Only one year, 1997, had no recordings of possible *R. temporaria*.
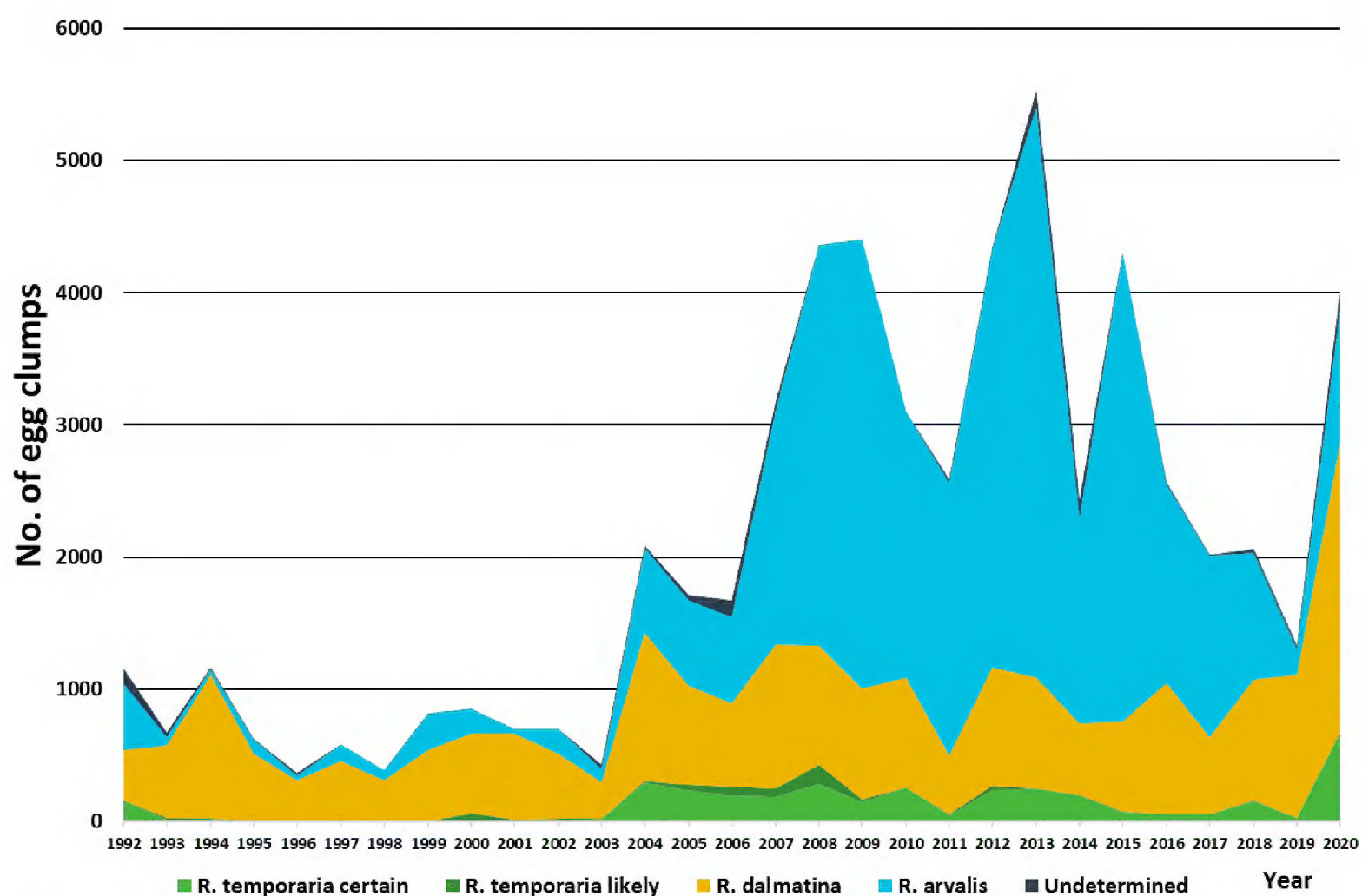

Figure 2. Total annual egg clump numbers from 1992 to 2020. From the bottom to the top, the sections of the graph show the figures for certain *R. temporaria*, likely *R. temporaria*, *R. dalmatina*, *R. arvalis* and egg clumps not determined by species. A few ponds were omitted in 1992 and a few others, in 1993. Data for these ponds were extrapolated from the general trends for each species in those years, in order to give a correct impression of the relative change from year to year during the whole study period. Without the inclusion of the extrapolated values, the total number of egg clumps would have been 18% lower and 7% lower than actually shown in 1992 and 1993, respectively.

The simultaneous increase in all three species from 2004 onwards is remarkable. The increase was not restricted to a few waterbodies, but was observed in many waterbodies all over the study area. There was an additional increase of *R. arvalis* from 2007 onwards, leading to a population size about 100 times higher than at the minimum in 1994. This increase, too, was distributed over many waterbodies.

The geographic pattern of colonisation

Rana dalmatina was recorded in all waterbodies in the study area at least once and colonisation of new sites took place rapidly (Fig. 3). Only a few waterbodies were situated far from a possible source locality.

In *R. arvalis*, no single waterbody was occupied every single year during the first study years. However, those seven waterbodies that were most permanently occupied, all situated in the west-central area, could be considered as likely source ponds (Fig. 4). Out of the 19 "target lo-

calities" that were available for permanent colonisation, 17 were eventually colonised. One was never visited by the species and one had eggs only in a couple of years, after which the species disappeared again.

In *R. temporaria*, no waterbodies were obvious source ponds. In some ponds, the species was absent during the mid-1990s for no longer than 3 or 4 years and the few individuals present may have shifted between some of these ponds. These are situated in the mid-central area (Fig. 5). Colonisers of other waterbodies may or may not have originated from these localities. Out of the 19 "target localities" that were available for permanent colonisation, three had no recordings of *R. temporaria*. All other "target localities" were either colonised or had sparse visits of the species.

The temporal aspects of colonisation

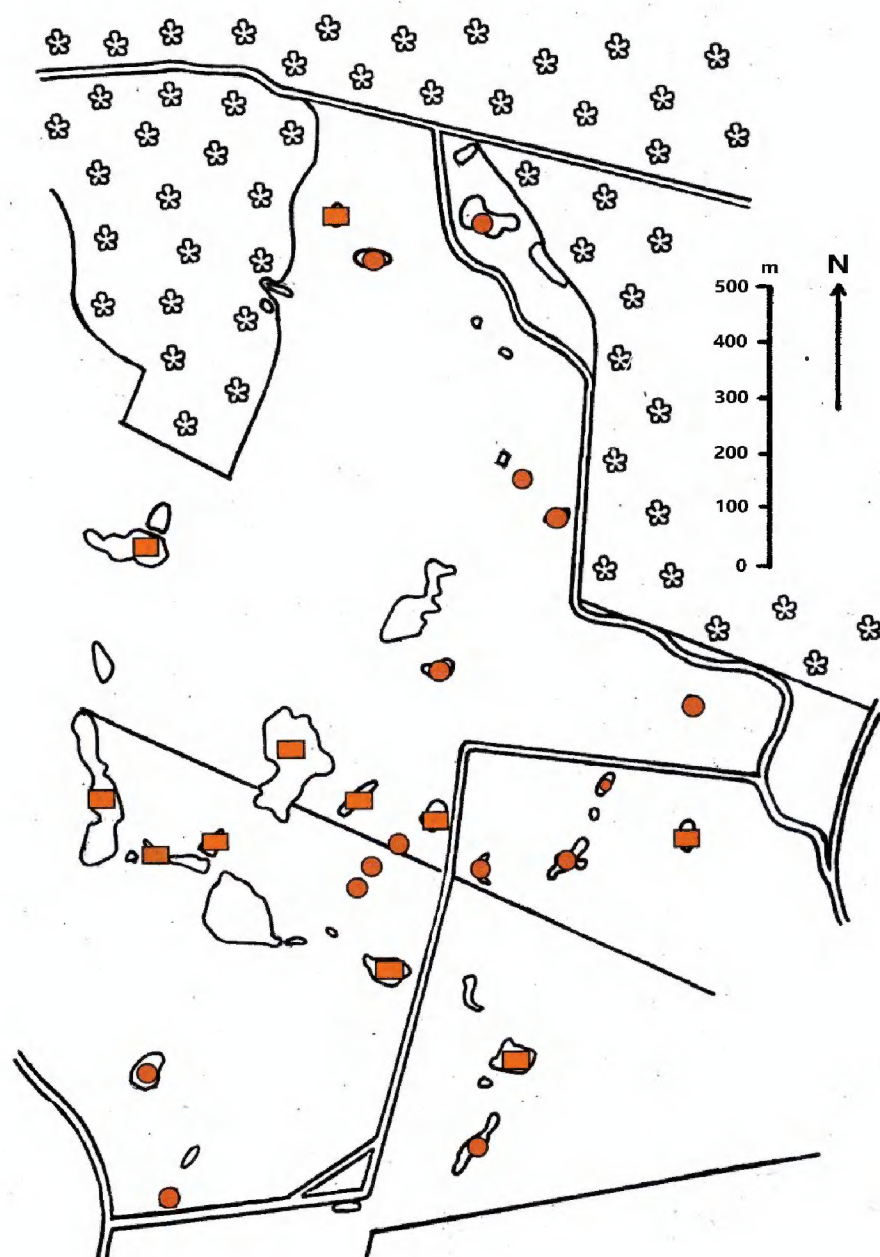The average length of the period from the time when the first eggs could potentially appear until the time when

Figure 3. Map of the study area illustrating colonisations of *R. dalmatina*. Surrounding woods are shown. Any waterbodies existing at some time are shown with their outlines. Coloured rectangles show likely source localities. Circles indicate the 15 "target localities" that were available for permanent colonisation. Larger circles indicate permanent colonisation within 0–5 years. There is one smaller circle in the east-central area where colonisation occurred only after 8 years.
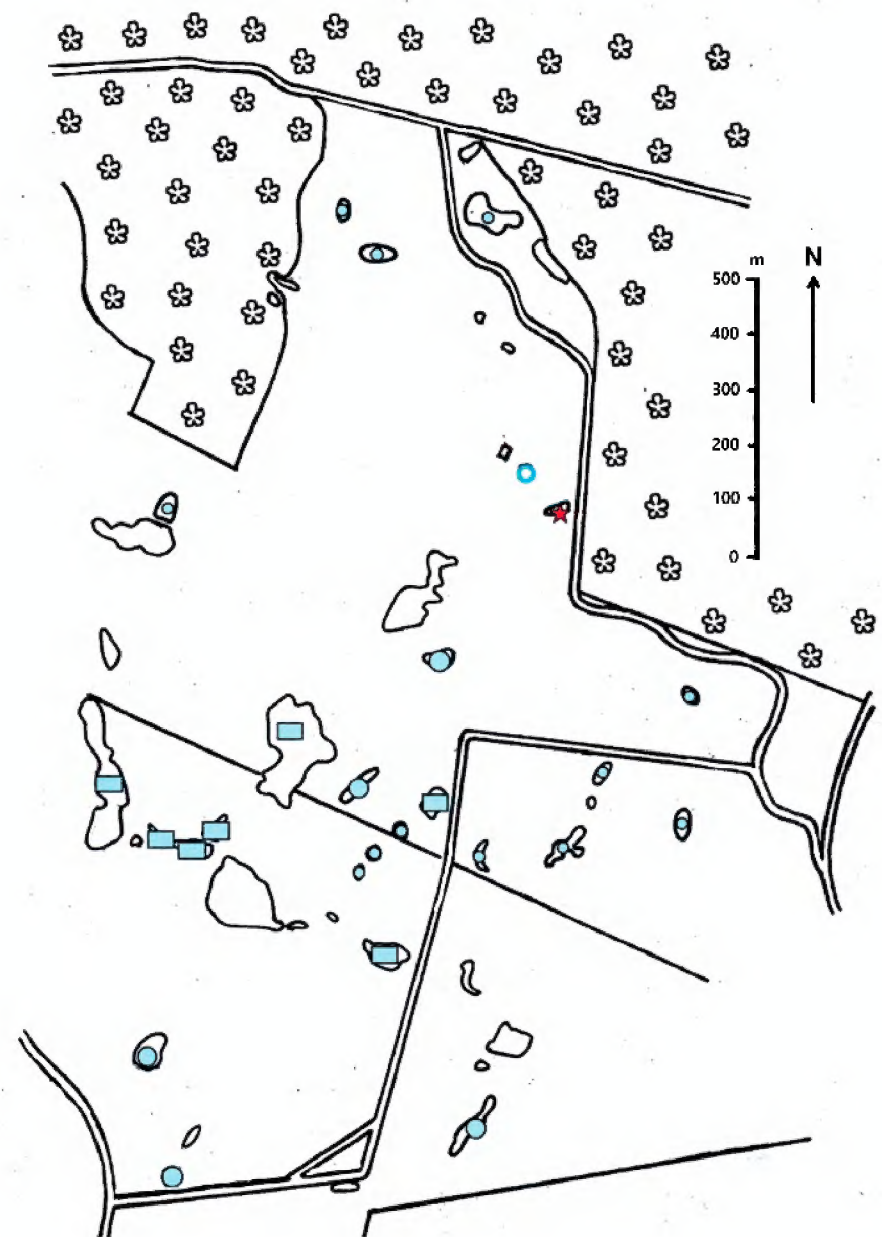

Figure 4. Map of the study area illustrating colonisations of *R. arvalis*. Coloured rectangles show likely source localities. Filled circles show colonised "target ponds". Larger circles indicate permanent colonisation within 0–5 years, smaller circles permanent colonisation after more than 5 years. An open circle (north of the red asterisk) indicates that eggs had been found there, but colonisation was not permanent. A red star shows a "target pond" where the species never appeared. The species also colonised some other (older) ponds, which were not target ponds (not shown).
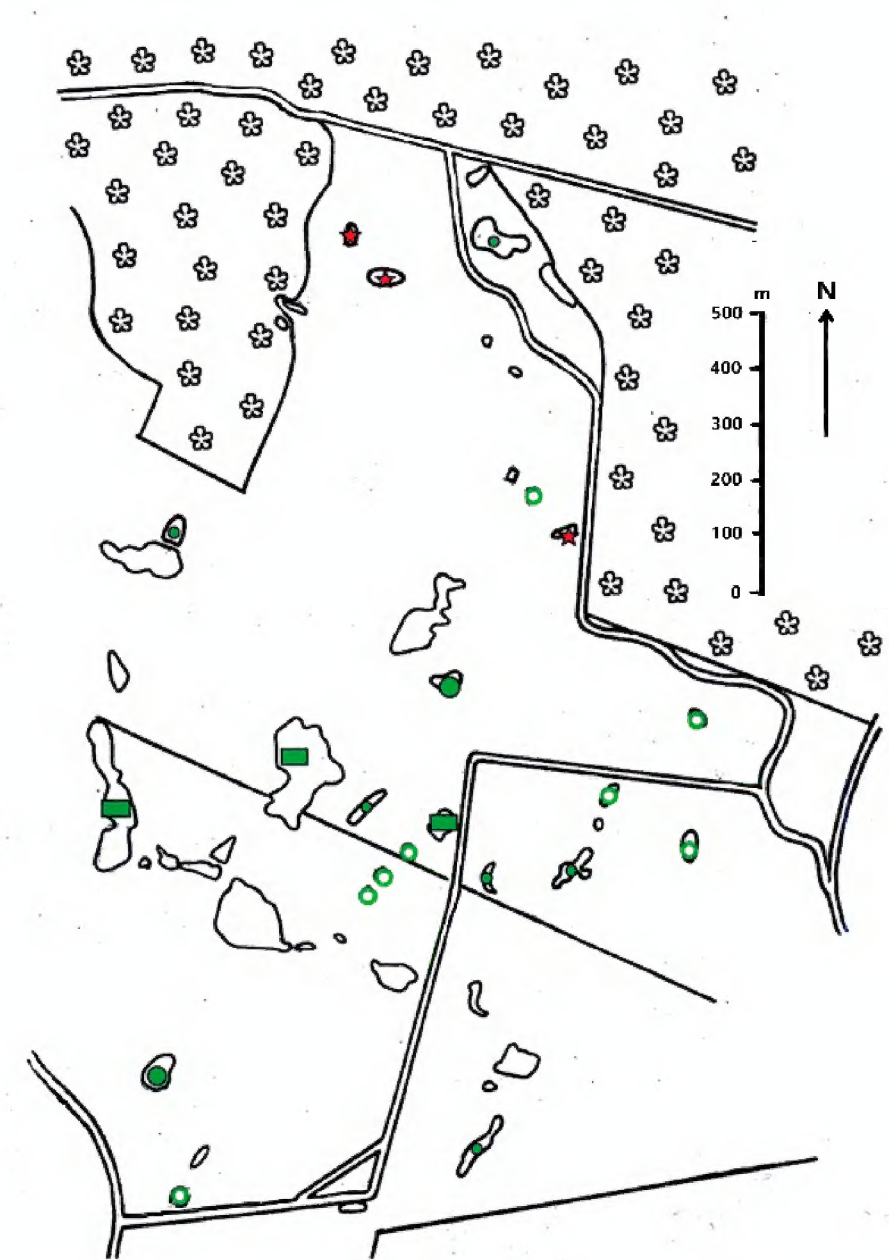
Figure 5. Map of the study area illustrating colonisations of *R. temporaria*. Coloured rectangles show likely source localities. Filled circles show colonised "target ponds". Larger circles indicate permanent colonisation within 0–5 years, smaller circles permanent colonisation after more than 5 years. Open circles indicate that eggs had been found there or a single adult had been observed, but colonisation was not permanent. The three red stars show "target ponds" where the species never appeared. The species also colonised some other (older) ponds, which were not target ponds (not shown).

the first egg clumps actually appeared differed between species. *Rana dalmatina* usually appeared in the very year that occurrence became possible. *Rana arvalis* and *R. temporaria*, on the other hand, usually arrived much later. In many cases, more than 10 years elapsed before the first eggs appeared (Table 1). In those new waterbodies where the species appeared, the average duration until egg clumps appeared for the first time was 0.5 years (SD 1.2) for *R. dalmatina*, 7.9 years (SD 5.8) for *R. arvalis* and 10.6 years (SD 6.9) for *R. temporaria*.

Table 1. Time to first appearance of eggs after a water body had become available for colonisation. Each cell gives the number of water bodies with first appearance after the number of years indicated in the headline atina.

Species	Number of years							No eggs found
	0	1–2	3–5	6–10	11–15	16–20	> 20	
R. dalmatina	11	3	1	0	0	0	0	0
R. arvalis	1	3	3	5	3	3	0	1
R. temporaria	0	1	4	2	4	2	2	4

However, the first egg clumps did not necessarily indicate the beginning of a more permanent colonisation. The species would often be absent for more than three consecutive years after the first colonisation event and more permanent colonisation would only occur later. *Rana dalmatina* colonised all waterbodies and no colonisation was delayed more than 8 years, whereas, in the other two species, about half of the colonisations were delayed more than 10 years. Two waterbodies were not permanently colonised by *R. arvalis*. Eleven waterbodies were not permanently colonised by *R. temporaria* (Table 2). For those waterbodies that were colonised, the average duration until a colonisation lasting for at least several years was 0.9 years (SD 2.2) for *R. dalmatina*, 10.5 years (SD 6.6) for *R. arvalis* and 13.4 years (SD 8.8) for *R. temporaria*.

Table 2. Time taken to colonise water bodies by the three frog species. Each cell gives the number of water bodies that were colonised after the number of years indicated.

Species	Number of years							Not colonised
	0	1–2	3–5	6–10	11–15	16–20	> 20	
R. dalmatina	10	3	1	1	0	0	0	0
R. arvalis	1	2	2	3	4	4	1	2
R. temporaria	0	1	1	2	1	2	1	11

The difference between *R. dalmatina* and the two other species in length of period until first appearance was highly significant. The same was true for the difference in length of the period until colonisation (Wilcoxon-Mann-Whitney test: all comparisons: $p < 0.0001$). In contrast, the difference between *R. arvalis* and *R. temporaria* was not significant ($p = 0.14$ for first appearance, $p = 0.48$ for colonisation).

This is true when analysing the whole study period. However, the opportunities for colonisation by *R. arvalis* and *R. temporaria* were relatively poor in the first half of the study period, whereas *R. dalmatina* had relatively better opportunities to colonise the northern waterbodies rapidly, because it was already present from the beginning in both the southern and the northern half of the study area (Fig. 3). *Rana arvalis* and *R. temporaria* had small populations until 2004 (Fig. 2). The situation for these two species was much better in the second half of the study period. Therefore, a second analysis was made to see if the differences between the species in the rate of colonisation persisted in the second half of the study period. This analysis was restricted to those waterbodies that were available for colonisation from 2004 onwards (number of available vacant waterbodies that were eventually colonised: *R. dalmatina*: 7; *R. arvalis*: 9; *R. temporaria*: 6). This new analysis showed the same pattern as the analysis for the whole period. *Rana dalmatina* still appeared earlier than *R. arvalis* and earlier than *R. temporaria* ($p < 0.0005$ resp. $p = 0.02$) and *R. dalmatina* also still colonised earlier than *R. arvalis* and *R. temporaria* ($p < 0.05$ in both comparisons).

In years with large population increases, some of the many new individuals may colonise new waterbodies. To

examine if colonisations occur mainly as a result of population growth, I identified years in which a marked population rise occurred, applying the criterion described in the Methods section. Years with a large population rise or boost were for *R. dalmatina*: 1994, 2004, 2007, 2012 and 2020; for *R. arvalis*: 2007, 2008, 2012, 2013, 2015 and 2020; and for *R. temporaria*: 2004, 2008, 2012, 2018 and 2020. For *R. arvalis*, there was a significant trend that events of first appearance occurred in the boost years more often than expected (eight events out of 18; the occurrence of eight events or more has a probability of p = 0.0153). Likewise, concerning colonisation events, the figures are eight events out of 17, p = 0.0103. A similar pattern could not be demonstrated for the other species. Considering that three species were tested and one had a significant trend, we may apply a Bonferroni correction with a factor 3, giving the criterion that p < 0.05/3 = 0.0167, which is met for *R. arvalis*. In *R. temporaria*, there was a slight trend for first appearances to occur relatively frequently in boost years (p < 0.25) and also for colonisations of non-target localities to occur in boost years (data not shown). In contrast, there was no such trend in *R. dalmatina*. It appeared in many waterbodies in the very first year that they existed, most often in 1993, when its total population was relatively small. Therefore, what governed colonisations by *R. dalmatina* was availability of colonisable waterbodies, not the population size.

Temporary waterbodies

Some egg clumps were found in temporary floodings that did not hold water long enough to allow for successful breeding and that did not develop into more permanent ponds over the years. The total number per year of egg clumps deposited in such places was, on average, 12.2 for *R. dalmatina*, 14.9 for *R. arvalis* and 0.6 for *R. temporaria*. In addition, some egg clumps were found in water-filled wheel tracks made by heavy military vehicles. The average annual number egg clumps deposited in such places was 4.1 for *R. dalmatina*, 1.1 for *R. arvalis* and 0 for *R. temporaria*.

Local extinctions and pond shifts

Once *R. dalmatina* had colonised a waterbody, it nearly always remained there, except for years when the floodings had no water. Out of 15 suitable waterbodies existing from the start of the study, 10 contained *R. dalmatina* eggs every single year from 1992 to 2020. There were just two cases when the species disappeared from a pond due to gradual overgrowth with shading bushes. In one other pond, a target pond, the population size went from a record-high 494 egg clumps in 1994 to just 2 egg clumps in 2020. The main cause of this was probably that pikes had appeared there at some time after the pond was excavated.

For *R. arvalis* and *R. temporaria*, the pattern was different. There were just five waterbodies with stable occurrence of *R. arvalis* from 2004 onwards. Out of 15 permanently suitable waterbodies, existing from the start of the study, none contained *R. arvalis* or *R. temporaria* eggs every single year from 1992 onwards.

In some cases, *R. arvalis* or *R. temporaria* showed a very erratic course of colonisation. They suddenly appeared in a waterbody and spawned a large number of egg clumps there, but then were absent for a long period afterwards, even if the spawning had led to breeding success. *Rana arvalis* often colonised a pond preliminarily, then it was absent, often for 4 years or more and then colonised the pond again. In some cases, such local extinctions were synchronous between several ponds. In *R. temporaria*, there were many shifts between two or three neighbouring waterbodies, situated 100 – 200 m from each other, with breeding in one waterbody one or two years and in another in one or two other years. Many local extinctions were followed by subsequent recolonisations, but rarely in a synchronous pattern.

Repeated censuses of the same waterbodies

In those cases when all egg clumps in a waterbody were counted twice, the results were mixed. For *R. dalmatina*, the change in numbers counted from the first to the second visit was as follows, with indications of the proportion of the egg clumps represented in each category: in 20%, a large increase (an increase by 50% or more), in 34% a moderate increase (on average 23%), in 5% practically identical counts (± 1 egg clump) and in nearly 40% a decline in the numbers (on average an 18% decline). The large increases were in cases when the first visit was obviously too early in the season.

In 1996, a late spring with no eggs yet on 09/04, *R. dalmatina* on average spawned later than the other brown frogs. *Rana dalmatina* egg clumps that were clearly newly spawned were found at a second visit on 05/05 after a first visit on 23/04, indicating that egg clumps were spawned in the end of April or the first days of May. In contrast, in some other years, the spawning season had ended in many waterbodies much earlier, in one particular year already before 24/03.

The data on repeated visits concerning *R. arvalis* are dominated by results from a particular year when there was much ongoing spawning during the first half of April after the first visit. Apart from that year, the change in numbers counted from the first to the second visit was as follows: waterbodies representing nearly 50% of the egg clumps showed moderate increases (23% on average) at the second count. For 9% of the egg clumps there were identical results (± 1 egg clump) and for 42% of the egg clumps, there was a decline in numbers (on average a 22% decline). There were no indications that large increases were preferably in cases when the first visit was relatively early in the season.

There are no useful data for *R. temporaria* on this aspect.

Another procedure was to record any additional, newly-spawned egg clumps observed at visits made late in the season. For *R. dalmatina*, this added on average 6% to the previous counts. This percentage was lowest (3%) when only 1–7 days had passed since the previous visit and largest (12%) when more than 20 days had passed since the previous visit. For *R. arvalis*, this procedure added on average 4% to the previous counts, with no trend regarding the number of days between the visits.

Discussion

Population trends

Considering that few long time series of amphibian populations have been published, it is relevant to present the population trends in the present study (Fig. 2). There was a large increase in all three species in 2004 and again a large increase especially for *R. arvalis* in 2007–2008. These increases were observed in many waterbodies simultaneously and, thus, could not be explained by events in a few specific waterbodies. Rather, they could be caused by some weather conditions, such as the unusually mild winter 2006–2007. Analyses of what weather conditions might explain the ups and downs during the study period will be possible and are planned.

There were no certain recordings of *R. temporaria* from 1995 to 2002, but in most of these years, there were likely recordings. To classify these likely recordings as "undetermined" would have given the false impression that *R. temporaria* was most likely absent during a long period, when it was actually most likely present. To determine an egg clump that looks like *temporaria* as certainly *temporaria* is not easy. It took some years' experience before I was able to conclude that feeling the firmness of the egg gel is the most reliable character. The problem is largest when there are very few such egg clumps. When there are more such egg clumps, it is easier to find additional evidence, for example to find egg clumps where the larvae have just hatched and can be determined from their gill branches.

When "certain *R. temporaria*" appeared from 2003 onwards, they might possibly have immigrated from sites outside of the study area. However, they had more likely been present in low numbers in the area all along. In spite of the apparent lack of any adults in 1997, a few juveniles may have survived to breed as three-year olds in 1998 or 1999.

Different rates of colonisation

In my view, all the pre-defined target ponds were equally suitable for all species, being newly formed and not yet densely grown in with swamp vegetation or willow bushes. Except for one pond where a pike was observed, they were all free from fish, having no connection to other waterbodies. If there were a difference in suitability for the different species, then most of them should be most suitable for *R. arvalis* and *R. temporaria*, because most of them were floodings with shallow zones of flooded grass vegetation, which is optimal for them.

In the study area, *Rana dalmatina* was a much more efficient coloniser of newly-available waterbodies than the other two species. It colonised most waterbodies at once when they arose or became suitable, in years when the total population had declined, as well as in years with an increase. Colonisation events in *R. arvalis* and *R. temporaria* occurred after much longer periods and mostly in years with a considerable general population increase. In these years, strong cohorts of juveniles must have survived until sexual maturity, so it may be assumed that the colonising individuals were first-time breeders.

In general, in animal populations, there will often be some individuals with high site fidelity and other individuals with low site fidelity, and this has been documented also in a few amphibian species (Denoël et al. 2018). If all individuals had high site fidelity, the species would never spread. Could the proportion showing site fidelity differ between species, thereby explaining the higher colonisation ability in *R. dalmatina*? The available evidence is that *R. dalmatina* individuals do not show less site fidelity to their natal pond than the two other species. A German study of newly-metamorphosed *R. dalmatina* that were individually marked (Kneitz 1997) showed that, two years later, 80–90% of the recaptured individuals had returned to their natal pond. Amongst the adults that were equipped with a transponder, nearly 100% returned to their breeding site. Hachtel et al. (2005) found that the percentage of marked adults that returned to the same breeding pond after one year was higher in *R. dalmatina* (51%) than in *R. temporaria* (23–26%).

In the present study, *R. dalmatina* populations were more stable from year to year than were the populations of *R. arvalis* and *R. temporaria*. In 10 out of 15 suitable waterbodies, *R. dalmatina* spawned in every single year. The tendency for frog populations to shift breeding site entirely from one year to the next was most marked for *R. temporaria*, even though this species spawned more rarely in temporary waterbodies than the two other species.

Data from other studies may confirm the trend for relatively stable occurrence in *R. dalmatina*. On the Swedish island of Öland, Ahlén (2013) monitored *R. dalmatina* breeding sites continuously over 20 years. Out of 150 ponds with the species, it spawned every single year in 53% of them. In comparison, in a moist forest area in Bavaria, Grözinger et al. (2012) monitored *R. temporaria* continuously during 7 years. Out of 43 ponds with the species, only 10 (23%) contained spawn every single year.

Movement patterns

Several types of evidence indicate that differences in movement patterns partially explained the different colonisation rates of the three species. Although the majority

of individuals stay relatively close to their site of origin, evidence from a number of amphibian species showed that a few individuals migrate away over very large distances, in many species more than 10 km (Smith and Green 2005). Sinsch (2014) noted: "Theory predicts that juveniles should move farther, faster and more frequently than adults". Therefore, it is relevant to discuss what is known about the movement patterns of juveniles of the three species of brown frogs treated here. Kneitz (1997) found that marked *R. dalmatina* juveniles moved an average of 26 m/day or 1 km in 8 weeks. He added that juveniles are of great importance in the expansion and colonisation of new habitats.

Unpublished observations made by the author in the study area and elsewhere in Denmark show that newly-metamorphosed froglets of the three species do not move equally quickly away from their natal pond. *Rana temporaria* moves faster away from the water than *R. arvalis*, but *R. dalmatina* moves even faster. At a pond in Kulsbjerge, studied at ten dates in June and July 2009, many newly-metamorphosed *R. dalmatina* moved 15–30 m into the surrounding dry land even when they still had remains of their tail and very few older froglets remained within 10 m from the water's edge, even when the weather was dry. Newly-metamorphosed *R. arvalis* and *R. temporaria* stayed for a relatively long time in the water or within 2 m from the water's edge. Moreover, even when their tail had been resorbed, it was only after rainy weather that they moved further away from the water's edge than 15 m.

Unpublished data about the habitats of young brown frogs in their first year of life (n = 106 for *R. temporaria*, 41 for *R. arvalis* and 56 for *R. dalmatina*) were gathered by Per Holm Andersen in Denmark in the 1940s (cf. Fog (1988)). About half of the newly-metamorphosed *R. dalmatina* were found far from a pond (i.e. no presence of a pond was mentioned), which was true of very few *R. temporaria* and of no *R. arvalis*. For the juveniles of a few months of age, the proportion still found near breeding sites was 83% for *R. arvalis*, 61% for *R. temporaria* and 13% for *R. dalmatina*. This pattern was even more pronounced for juveniles after their first hibernation, whereas some adult *R. dalmatina* were found close to ponds. Consequently, it is likely that juvenile *R. dalmatina*, emigrating quickly from the pond, disperse rapidly and widely in the landscape. However, they may also have a high degree of philopatry, i.e. although they move far away, most of them return to their natal ponds, which is confirmed by the relatively high stability of *R. dalmatina* breeding populations.

A paradoxical relation may exist between site fidelity and long-range movements. Those moving far away may have a strong need to return exactly to their point of origin. Juveniles of the two other species do not leave the area around the breeding pond as quickly. When they reach adulthood, after having moved around, they may most often choose a breeding site in, or in the vicinity of, their natal pond. They may do so not just because of philopatry, but also as a consequence of not having moved far initially.

Altogether, the pattern that emerges is that most *R. dalmatina* individuals return as adults to their natal ponds after having moved far away as younger individuals. Even so, 10–20% settle elsewhere and breed in other ponds (Kneitz 1997). Once they have chosen a new pond, they may show a high degree of site fidelity to the new site as indicated by the relatively high stability of *R. dalmatina* populations in new ponds. In the two other species, the whole process is probably more random. The frogs do not move as far away, that is, the need for a strongly-developed philopatry is not as strong as in *R. dalmatina*.

If these are the three species' movement patterns, this would explain the observations made here. In *R. dalmatina*, a relatively more constant proportion of the juveniles emigrate to other sites and, therefore, a high likelihood of colonisation exists even in years with a low surplus of emigrating juveniles. The emigration process is less strict in *R. temporaria* and *R. arvalis*; only in years with a large surplus of juveniles will many of them settle in new ponds due to random movements.

The data do not allow conclusions on how far colonising frogs have migrated because we do not know their precise origin. Furthermore, some may have originated from waterbodies outside the study area. Two of the waterbodies in the north of the study area were colonised by *R. arvalis* in 2008, when the distance from both of these to the nearest possible source locality was about 660 m. The most isolated target pond, located furthest to the southwest, was colonised by *R. dalmatina* after a 2–year period, by *R. arvalis* after a 3–year period and probably by *R. temporaria* temporarily after a 4–year period. It has a distance of 530 m to the two nearest possible source ponds within the study area and a distance of 510 m to the nearest possible source pond outside of the study area. A few other relatively isolated waterbodies have distances to possible source ponds in- and outside of the study area of slightly less than 500 m.

Other evidence on different colonisation rates

The results of the present study agree well with the impression that the author and other herpetologists have concerning brown frogs in Denmark — *R. arvalis* and *R. temporaria* colonise relatively slowly, whereas new ponds are very often colonised by *R. dalmatina* surprisingly rapidly, even over considerable distances. Other evidence supports this assertion. Out of 66 newly-created or restored ponds from different parts of Denmark, *R. dalmatina* had colonised 65% within 5 years, which was a higher percentage than for five other anuran species comprised by the same study (Fog 1997a).

Evidence from the Bonn area, Germany, agrees that *R. dalmatina* is a fast coloniser (Hachtel and Grossenbacher 2014), but it generally does not agree that *R. temporaria* is a slow coloniser, especially not where *R. dalmatina* does not occur. In a study in the Netherlands, *R. tem-*

poraria turned out to be the best coloniser out of eight amphibian species: this species already occurred in 72% of the newly-created ponds two years after construction (Laan and Verboom 1990). In another Dutch study, just above 50% of the two-year old ponds had been colonised by *R. temporaria* (Stumpel and van der Voet 1998). In a region of south Sweden, *R. arvalis* and *R. temporaria* both colonised 19 out of 21 new ponds within 2–6 years; *R. arvalis* was more dependent than *R. temporaria* on the proximity of a source population within 250 m (Almhagen 2007). Furthermore, *R. arvalis* generally moves shorter distances than the other species do (Glandt 2014).

The present study suggests that some species or some local populations of amphibians colonise much more slowly than others. This may be of concern when new ponds are made in efforts to save amphibian populations. It may possibly differ from one region to another precisely what species are poor colonisers.

The situation in the landscape in general

In other parts of South Zealand, in the agricultural landscape, *R. dalmatina* is also widespread, whereas *R. arvalis* and *R. temporaria* are in a much worse situation there than in the military training area. In recent decades, *R. arvalis* and *R. temporaria* have declined drastically in large parts of South Zealand (Fog, unpubl. data), whereas *R. dalmatina* has expanded (Fog 1997b). Recordings of 152 ponds in a 1 km wide zone along the coastline of South Zealand made by the author in 2016 yielded the following number of breeding sites: *R. dalmatina* 47, *R. arvalis* 11 and *R. temporaria* 3.

Rana temporaria is rather sparsely present in southeast Denmark. The "common" frog is uncommon in this part of Denmark. It is completely absent from all the south-eastern islands, including Lolland, Falster and Møn with a combined area of 2,935 km² (cf. Fig. 1). Falster and Møn are both situated just 8 km from Kulsbjerge. That *R. temporaria* is absent from all islands in southeast Denmark is contrary to what is stated in Gollmann et al. (2014: 318), but the statement there is false due to an erroneous translation of their source, Bringsøe and Graff (1995). *Rana arvalis* has declined considerably in recent years on these islands, whereas *R. dalmatina* is widespread there.

Furthermore, there is evidence in recent decades that *R. dalmatina* advances where the other two species retreat. This is most clear in the peninsula of Knudshoved Odde, a nature area in South Zealand with many ponds. Here, the situation in 1946 was that only *R. arvalis* and *R. temporaria* were present, whereas *R. dalmatina* occurred in a forest approx. 4 km from there (H. Volsøe, unpubl. data). From the 1980s and onwards, *R. dalmatina* migrated to the peninsula and colonised all ponds there, whereas *R. temporaria* and *R. arvalis* disappeared completely.

The trend that *R. dalmatina* advances in the coastal regions of south Zealand, whereas the two other species are retreating, may partially be explained by the large in-crease of herons there, which are now extremely numerous predators in some amphibian ponds. Sometimes they may completely exterminate a breeding colony of brown frogs. They are a threat to breeding *R. arvalis* and *R. temporaria*, which are active in the water surface at daytime. They are not a threat to breeding *R. dalmatina*, which are active only under the surface during night.

In recent decades, *R. arvalis* and *R. temporaria* have declined so much in this part of Denmark that their continued presence may be threatened. Therefore, the situation in the military area is remarkable. Both these species have survived a period of very low population size there and have then expanded greatly. Evidently, the military training ground which is an open landscape without agricultural utilisation is much more favourable to these species than the surrounding farmland. Kulsbjerge has become at kind of sanctuary for these amphibian species (as well as for *Hyla arborea*). This exemplifies the importance of large uncultivated areas in amphibian conservation.

Uncertainties and sources of error

The probability of detecting egg clumps was unknown. Schmidt et al. (2023) showed that the largest variation in detection probability (presence/absence) of amphibian species was among-observer heterogeneity. In the present study, all observations have been made by the same person and under the same weather conditions. Thus, differences between years are reliable indications of differences in the population size, so it is justified to consider the counts as an index variable. One study from southern Europe indicates that about 93% of all *R. dalmatina* egg clumps were detected by one observer as a percentage of those detected by another observer on the same day (Falaschi et al. 2022). However, the study by Falaschi et al. (2022) did not specify weather conditions, vegetation density or water clarity, all of which may be of importance. In general, a risk exists that some egg clumps are hidden from the observer's view in waterbodies with dense swamp vegetation, turbid water and/or deep water (Hachtel and Grossenbacher 2014). Therefore, the detection probability is not necessarily the same in all waterbodies. However, in the present study, vegetation and turbidity changed little from year to year, so results for a given waterbody will be comparable between neighbouring years.

If counts were made too early in the season, eggs that had been spawned late would have been missed and the numbers counted would be too low. This introduced an error margin of unknown size. However, those cases with a large increase at the second visit in counts of *R. dalmatina* were cases where the first visit had clearly been made much too early in the season. Inspecting the dates confirmed that, in these cases, the first visit had been made relatively early, in the period 30/03–06/04, and had always been followed by a later visit. When the first visit to a waterbody was made relatively late in the season, then the last visit yielded only a moderate number

of additional egg clumps – on average about 23% more in *R. dalmatina* and likewise, 23% more in *R. arvalis*. The hypothetical further increase after the last visit must have been smaller than this, which is also suggested by the recordings of only few newly-spawned egg clumps at the last visit. The change in population size from one year to the next, on average for all 28 comparisons of two neighbouring years, were as follows: The counts differed by a factor of 1.52 for *R. dalmatina*, 2.48 for *R. arvalis* and 2.78 for certain + likely *R. temporaria*. Relative to this, an adjustment by a factor less than 1.23 for late eggs gives an uncertainty less than the average change from year to year. Therefore, this uncertainty does not severely affect reported changes from year to year.

Acknowledgements

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Supplementary material 1

Raw data file

Authors: Kåre Fog

Data type: xlsx

Explanation note: Numerals indicate the number of egg clumps. If a cell is empty, it was not relevant to investigate the waterbody, for example, if it did not exist yet or did not exist in that year. "Dry" indicates that the waterbody was practically dry when investigated. This concerns cases when a waterbody holds water in most other years and so is believed to harbour an otherwise permanent population, which then has to move to another waterbody in that particular year. NI means Not Investigated. 0 means that the waterbody was investigated, but no eggs of that particular species were found. X means the species was present and spawned, but the eggs were not counted. Waterbody numbers refer to the map of the study area, with all 46 waterbodies shown. Names of waterbodies are the names used by the author.

Link: https://doi.org/10.3897/herpetozoa.37.e107986.suppl1

Supplementary material 2

Map with labelled localities

Authors: Kåre Fog

Data type: pdf

Explanation note: Map showing the waterbody numbers used in the raw data file (Suppl. material 1).

Link: https://doi.org/10.3897/herpetozoa.37.e107986.suppl2